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OBSERVATIONS ON THE BIONOMICS OF ANOPHELES.*

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THE striking recedence of malaria in certain portions of the world and its equally noticeable extension in others are still in part unexplained phenomena, and offer a field for investigation that involves a consideration of many strictly biological problems. Viewed in its broader aspects, the successful conduct of a campaign against malaria rests upon a proper comprehension of the relation of three organisms belonging to widely separated groups of the animal kingdom. The importance of understanding the biological or ecological features of the problem can hardly be overestimated. The possible existence of natural causes favoring or hindering malaria is a matter upon which studies in the field may be able to shed light. An instance of the fruitful outcome of general observations is found in Theobald Smith's[1] suggestive remarks on the natural history and probable mode of spread of tertian malaria in Massachusetts. With these points in mind the writers have undertaken a series of detailed observations on the bionomics of the malaria-bearing mosquito.

The following observations on Anopheles have been carried out partly in the vicinity of Chicago, partly in a small country town in western Michigan (Eastmanville, about twenty miles west of Grand Rapids), and partly in a locality in New Hampshire (Shelburne) already described by one of the writers.[2]

Anopheles larvæ were collected at thirty-four different points in and about Chicago, including thirteen stations within the city limits. Breeding pools were found in all quarters of the city, and in the suburbs on the north, west, and south sides. The adult mosquitoes sometimes invade rather thickly settled parts of the city, and have been captured in houses within two blocks of

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[1] *Bost. Med. and Surg. Jour.*, 1903, 149, p. 57.

[2] *Jour. Med. Research*, 1902, 7, p. 1.

the University of Chicago campus. The dominant species raised from larvæ taken in this vicinity has been A. punctipennis. In 1902, 59 individuals belonging to this species were bred, 29 of which were males and 30 females, while only 19 individuals of A. maculipennis developed (5 males, 14 females). In 1903 the number of the latter species was much smaller (A. punctipennis, 32 males, 50 females; A. maculipennis, 1 male, no female). A. punctipennis seems to be the more common species in eastern Massachusetts,[1] as is also the case in at least one region in northern New England.[2] A record kept of the breeding places about Chicago, and the species developing from the larvæ captured showed that in four different bodies of water the larvæ of the two species were found together. Those reared from the larvæ and pupæ captured were divided between the two species as follows:

TABLE I.

Locality Number	A. punctipennis	A. maculipennis
5....................	4	1
9....................	15	5
14....................	1	1
17....................	1	8

Larvæ collected from seven different stations yielded A. punctipennis alone, while those collected from four stations produced only A. maculipennis. Our observations afford no reason for believing that the larvæ of A. maculipennis are reared with any more difficulty under artificial conditions than those of A. punctipennis. In fact it appears from our experience that larvæ that are 6–7 mm. in length when captured almost always pupate and develop normally when afforded ordinary care and attention. The figures given above are based entirely upon the results of raising these larger larvæ and pupæ. As a matter of fact, in western Michigan, where A. maculipennis was the more abundant form, no difficulty was experienced in rearing the larvæ. The disparity in the numbers of the two species bred from larvæ and pupæ must therefore be regarded as indicating the relative scarcity of A. maculipennis in the vicinity of Chicago, and in the neighborhood of Shelburne, N. H.

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[1] *Bost. Med. and Surg. Jour.*, 1903, 149, p. 88.

[2] *Jour. Med. Research*, 1902, 7, p. 1; cf. also DYAR, *Proc. Entomol. Soc. Wash.*, 1903, 5, No. 2.

In the third locality studied (western Michigan), A. maculipennis was by far the more common species, as shown in the following tables:

TABLE II.

	Imagoes Captured			
	A. maculipennis Males	A. maculipennis Females	A. punctipennis Males	A. punctipennis Females
1902...............	75	122	2	9
1903...............	42	156	2	5
1904...............	295	436	8	11

TABLE III.

	Bred from Larvæ and Pupæ			
	A. maculipennis Males	A. maculipennis Females	A. punctipennis Males	A. punctipennis Females
1903...............	33	32	1	4
1904...............	22	21	13	15

The distribution of the two species is a matter of some interest, since it has been proved that there is probably a difference in their ability to transmit malaria. A. maculipennis is the dominant species in Italy, Greece, Spain, and parts of France, and according to Laveran,[1] plays throughout Europe the most important rôle in the propagation of malaria. A. punctipennis is confined to North America. An attempt made by Berkeley and Smith[2] to infect A. punctipennis led to no definite outcome; Hirschberg[3] has since conducted more elaborate experiments upon the two common species of Anopheles by feeding them with the blood of patients known to contain the parasite of aestivo-autumnal malaria. The following results were obtained:

[1] *Comp. Rend. de la Soc. de Biol.*, 1904, March 4, p. 325.

[2] *New Jersey Agricultural College Expt. Station Rept.*, 1902, p. 512.

[3] *Bull. Johns Hopkins Hosp.*, 1904, 15, p. 53.

TABLE IV.

	Number Fed	Number Infected
A. maculipennis....	48	8
A. punctipennis.....	58	0

A similar difference in susceptibility to infection has been shown to exist between two common Anophelines in India, M. rossi and M. culicifacies (Christophers and Stephens).

Many localities in the United States show a marked disparity in the proportion of A. maculipennis and A. punctipennis. Bashore[1] found a preponderance of A. maculipennis (133 to 7) in a suburb of Harrisburg, Pa. Mention has already been made of the difference in the relative abundance of the two species in the localities observed by the writers, a difference furthermore that persisted through three seasons. A similar difference has been noted in the neighborhood of Boston (T. Smith) and Baltimore (Hirschberg). Hirschberg has pointed out that the distribution of the two species in the vicinity of Baltimore as previously determined by himself and Dohme[2] coincides in a general way with the occurrence of malaria-infected districts. The disease prevails where A. maculipennis has its breeding places, but is absent from districts where A. punctipennis abounds.

In but one of the three localities (Michigan) examined by us is A. maculipennis present in notable numbers. It may be remarked that this is also the only one of the three in which there is any history of marked malarial prevalence. The character of the region where A. maculipennis is found so abundantly is therefore of interest.

A. *The Locality.*—The observations were made in and about the village of Eastmanville, in western Michigan, during the summers of 1902, 1903, and 1904. A white settlement has existed at this point, upon the north bank of the Grand River, twenty miles (river measurement) from its debouchement into Lake Michigan, since about 1840. Prior to that date, and for some time afterward, Indians of the Ottawa and Pottawatomie tribes had villages near this part of the river. The population of the village, never more than a few hundreds, is at present about 150.

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[1] *Med. Record*, 1901, 59, p. 173.

[2] *Bull. Johns Hopkins Hosp.*, 1902, 13, p. 45.

The soil of the district is clay, covered by a few feet of sand for the most part, but occasionally cropping out. The country-side is almost entirely under cultivation or in pasture land; little or nothing remains of the marshes or of the heavy timber which formerly covered the area. The north bank of the river, upon which the village lies, rises with somewhat more marked declivity than the south, which is sandy, the channel being here, for two miles, on the north shore. The stream is at this point thirty rods wide; the vegetation of the shores is characterized by low willows and wild rice. North from the river run several ravines, dry in summer except for occasional spring-fed pools. Opposite the village, and separated from the river by a strip fifteen rods wide, part sand and part marshland, is a deep currentless bayou, mud-bottomed, spring-fed, ten rods wide and two miles long. With the exception of a few rods, its shores are timbered; the vegetation is that of a spring-fed lake.

B. *Malarial History.*—This part of Michigan was in earlier times, according to tradition, one of the worst malarial districts in a highly malarial state. No records except the general State Reports for western Michigan are available to show the former prevalence of malaria in Eastmanville, but the testimony of all the older settlers is unanimous. Everyone in the district was a sufferer, and everyone who came to the district expected to contract the disease. From the strongest of the laboring men to the infant born on the mother's ague day, the entire population was subject to chills and fever.

Such conditions do not now exist. The Michigan State Board of Health Reports contain interesting statistics regarding the decrease of malaria in Michigan during twenty-three years.

TABLE V.

WEEKLY REPORTS OF DISEASES IN MICHIGAN.

PER CENT. OF REPORTS WHICH SHOWED INTERMITTENT FEVER.

1877	75%	1884	65%	1891	36%	1898	19%
1878	82	1885	59	1892	27	1899	17
1879	82	1886	54	1893	24	1900	16
1880	82	1887	48	1894	24	1901	14
1881	82	1888	45	1895	22		
1882	71	1889	43	1896	19		
1883	69	1890	41	1897	17		

In 1879, 1880, and 1881, intermittent fever was the most prevalent of all diseases in Michigan; in 1881 the western division of the State, including the locality described above, showed a greater prevalence of malaria than other parts of the State, 90 per cent. of all weekly reports recording the disease as under the observation of the physician making the report. But according to the statements of local physicians the disease has been very infrequent in and about Eastmanville for the last few years. One physician had observed during six years but three cases presenting a typical malarial history; one of these occurred in the summer of 1889, one in 1902, and one in 1904. All three patients lived on the bank of the river, at distances of several miles from one another.

The question of course arises whether this decrease in malaria has been paralleled by a decrease in the number of the malaria-carrying mosquitoes.

In the absence of data, no definite statement can be made regarding the number and virulence of mosquitoes in the earlier years of the settlement, except the very general one that they were much "more numerous" than at present, and that they were very large. They were felt as so real a pest that the farmers would often leave the unscreened houses to sleep in the barns and haylofts, which were not frequented by the mosquitoes.

THE BREEDING-PLACES.

Stephens[1] has called attention to the practical importance of noting any difference in the breeding-grounds of the various species. In India M. culicifacies (known to convey malaria) "loves clear, fresh water of streams, rivers, canals, and other moving waters where it occurs in myriads," whereas M. rossi (probably not a malaria carrier) breeds only in shallow pools or puddles some inches deep. This difference in breeding habits naturally assumes high importance in any attempt to lessen malaria through destruction of breeding-places.

If there is a similar difference in the breeding-places of A. maculipennis and A. punctipennis, the task of restricting the spread of malaria in some regions may be materially simplified. In the present instance it was found that the favorite breeding-places of A. maculipennis and A. punctipennis, although close together, were of quite different character, as shown by the following facts relating to the distribution in Western Michigan.

Dipping for mosquito larvæ was carried out in the springs and spring-fed pools of the northern ravines, along the river shore, in the bayou, and in rain-water barrels of the village. In all of these places, with the exception of the bayou, Anopheles larvæ were found in abundance at some time during three consecutive summers. The distribution was more extensive in 1902, merely because the early part of the summer was wet, and water stood longer in the springs and ravines. In 1903 the early part of the summer was dry, so that by the middle of August two springs and the river shore only were left as breeding-places in the immediate vicinity of the village. In the river the larvæ of A. maculipennis are found regularly at certain places along the north shore, where abundant food and quiet are ensured by the wreckage and masses of river weed which lie a few inches below the surface of the water. Here, with the river running almost due west, the larvæ are exposed to direct sunlight. They were not found along the more shaded south shore. A curious instance of choice of breeding-places occurred in the summer of 1904 A small stream running to the river had, during the spring, a course of a mile or so down the ravine, but by August 1 it had dried to a few pools of the following character: (*a*) River inlet, 40 feet long and 7 feet wide, shaded by willows, bottom sand and mud, no larvæ; (*b*) Ten feet above this inlet a pool 40 feet by 4 feet in area, some 15 inches deep, entirely without shade or vegetation, no larvæ; (*c*) Only three feet from this second pool another pool of clear water, 5 feet by 3 feet in size, and 6 inches deep, shaded in the morning. Duckweed abounds here, and a quantity of green algæ cover the sticks and stones of the bottom; the pool swarms with Culex and Anopheles punctipennis larvæ; (*d*) Thirty-five feet above (*c*) is an "iron" pool with a deposit of iron; it is about 9 feet by 9 feet, 10 inches deep, partly shaded by bushes and a huge log. It contains no vegetation and no larvæ.[1] Of these four pools the smallest one, in the center of the row, is the only one containing Anopheles larvæ. *These larvæ are exclusively those of A. punctipennis, while in the river only a few feet from here, A. maculipennis is abundant.*

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[1] *Brit. Med. Jour.*, Sept. 17, 1904, p. 629.

Another noticeable feature of the distribution is the entire absence of all mosquito larvæ from the bayou, although the water is currentless, the vegetation abundant, and the light and shade favorable. It is probable that the duckweed and lily pads cover the surface too closely in the shallow water near the shore. As pool (*c*) above described became choked with duckweed later in the season, the larvæ disappeared.

The following table shows the undoubted selection of different breeding-places by A. maculipennis and A. punctipennis:

TABLE VI.

ANOPHELES BRED FROM LARVÆ AND PUPÆ.

	A. MACULIPENNIS		A. PUNCTIPENNIS	
	Males	Females	Males	Females
Collected from spring-fed pools	0	0	30	35
Collected from river	46	47	1	4

The fact that the breeding-places are only a few feet apart renders especially remarkable the specific preference displayed. The predominance of A. punctipennis in the other two regions that were examined is in accord with the observations in Michigan. A. punctipennis shows a predilection for spring-fed pools, and, in localities where these abound, is the chief species. Hirschberg and Dohme[2] observed a rather definite geographical distribution of the two species in the vicinity of Baltimore, A.

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[1] C. B. DAVENPORT has already mentioned the absence of larvæ in "iron" springs and in completely shaded pools, *Reports on Plans for the Extermination of Mosquitoes on the North Shore of Long Island, North-Shore Improvement Assoc.*, 1902, p. 40.

[2] *Loc. cit.*

maculipennis being found on low ground in or near large bodies of water, while A. punctipennis was found in small, clear streams or springs on higher ground.

DIFFERENTIATION OF LARVAL FORMS.

We have attempted to discover some morphological character that would serve to distinguish the larvæ of A. punctipennis from those of A. maculipennis but without obtaining any satisfactory criterion. The larval markings vary materially in different localities and at different seasons. In New Hampshire one of us was able to distinguish the two species by the markings on the larval head, but the larvæ collected by the same observer in the vicinity of Chicago permitted no such differentiation, the head markings being variable and non-characteristic. This seems also to be the case in Eastern Massachusetts and in New Jersey.[1] On the other hand Dyar,[2] who found in studying the mosquitoes on Long Island, New York, that no larval distinction between A. punctipennis and A. maculipennis was discoverable, did observe a well-marked difference between the larvæ of these species the next summer at Center Harbor, N. H.

> Curiously enough all the larvæ (of A. maculipennis) found were alike and of a peculiar striking coloration. They were at once separable from A. punctipennis by being black with a straight, narrow white dorsal line, furcate on thorax. The white spotted A. punctipennis were never marked with such a uniform line.

From these facts it would seem that larval markings are swayed to a large extent by local environmental causes, and cannot be uniformly depended upon for species differentiation.

DURATION OF LARVAL LIFE.

A number of observers have experienced difficulty in raising young larvæ to maturity.[3] It is undoubtedly true that unless considerable care be taken in regard to food, sunlight, and character of the water, the mortality among young larvæ (1.5–4 mm.) will be high. We have found, for instance, that water drawn from a spring through zinc-lined pipes has a decidedly toxic influence upon the larvæ and causes the death of many in a relatively short time. Water taken directly from the same spring has no such injurious effect. Ordinary city tap water is also an unfavorable medium. On the other hand larvæ may be reared easily by keeping them in porcelain dishes holding several liters of water, and by allowing the direct sunlight to strike them, though only for a small part of the day. If water dipped immediately from the pond in which the larvæ were captured is used to replenish the aquarium, the food supply will usually be adequate. In case food in large quantities is desired, we have found pleurococcus scraped from moist boards a convenient source of supply.

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[1] *New Jersey Agri. College Expt. Sta. Rep.*, 1902, p. 571.

[2] *Proc. Entomol. Soc. Wash.*, 1902, 5, No. 1.

[3] Cf. JOHNSON, *New Jersey Agri. College Expt. Sta. Rep.*, 1902, p. 373.

Under the suitable conditions just outlined, eggs laid in the dishes hatched with great regularity in three days at the ordinary summer temperature. The rapidity of growth of the larvæ developing from the eggs of a single laying is very uneven. Sometimes nearly a month may elapse between the first and the last pupation of one and the same brood. Our observations showed a larval life of thirty-six to sixty-one days for A. maculipennis and twenty-five to forty-eight days for A. punctipennis. These are somewhat longer periods than those noted by Howard,[1] Berkeley,[2] Nuttall and Shipley,[3] and others, but the observations of these writers seem to have been made at considerably higher temperatures (Berkeley, 34–36° C.) than those that prevailed during the conduct of our observations. Owing to the fact that the porcelain dishes used in our experiments were kept in the open, the temperature represented more nearly such conditions as exist in the small pools that form the natural breeding-places. The chilling of the water at night in these pools is greater than in housed aquaria. The duration of larval life appears, therefore, to be chiefly a function of temperature, and may vary under ordinary circumstances anywhere from fifteen days to two months. Nuttall and Shipley state that larvæ caught in the middle of

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[1] *Mosquitoes*, New York, 1901.

[2] *Laboratory Work with Mosquitoes*, New York, 1902.

[3] *Jour. of Hyg.*, 1901, 1902, 1903, 1, 2, 3.

August did not attain their full growth until November. It is yet a question whether the larvæ of A. maculipennis can hibernate. Those of A. bifurcatus can undoubtedly do so.[1]

PROPORTION OF SEXES.

As has been noted by all observers, the number of females captured is usually much larger than that of males. In the localities under our observation, the proportion of females to males among the captured adults (both A. maculipennis and A. punctipennis) is about two to one. This ratio does not, however, obtain among the insects bred from captured larvæ and pupæ; in any large series the numbers have been substantially equal. On this point our observations accord with those of Nuttall and Shipley, rather than with those of Rees.[2]

As a rule the larger larvæ develop into females and the smaller into males, as shown in the following records:

TABLE VII.

A. MACULIPENNIS.

Larval Length in mm.	Males	Females
7.5–8.0	0	12
7.0–7.5	8	10
6.0–7.0	5	0

These measurements were all made from freshly caught larvæ which pupated within four days after capture. From these facts the inference might seem legitimate that those larvæ which are supplied with abundant food, and consequently attain a larger size, develop into females, while those more scantily fed become males. It is quite possible, however, that other factors may enter into the problem. In every instance where a number of larvæ were bred from the egg under identical conditions in the same dish of water, the imagoes that appeared first were males and the later ones females. Rapidity of development and small size may be characters correlative with rather than determinative of sex. It seems clear that further observations are necessary.

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[1] *Jour. of Hyg.*, 1901, 1, p. 452.

[2] *Jour. of Hyg.*, 1902, 2, p. 68.

LONGEVITY OF THE IMAGO.

Captured mosquitoes, as many observers have shown, feed readily upon fresh slices of banana and other fruit. Captured females almost invariably live longer than males. Ordinarily death occurs within two weeks. This we found to be true even among females confined under natural conditions in a large cage (3.5 ft. × 3.5 ft. × 5 ft.) of mosquito netting in the open. The cage was supplied with fresh water and fruit, and the mosquitoes were sometimes given a meal of blood. Occasionally under these conditions life was maintained for a month even in midsummer. At a lower temperature in the ice-box (10°) life may be considerably prolonged. In one case three captured males (A. maculipennis) were placed in the ice-box on July 22; one died twelve days later; the other two were still alive after fifty-four days. One female (A. punctipennis) survived several transfers to room temperature (60–70°) during transportation from place to place, and lived sixty-three days. The two species, A. maculipennis and A. punctipennis, showed no discernible difference in respect to their longevity.

BITING HABITS.

As a rule, A. maculipennis does not bite until at least twenty-four hours after hatching, and it is usually true that active females cannot be induced to make an attempt to draw blood until from two to three days after emergence. The first trials, moreover, are not always successful. Johnson[1] states that in no instance was he "able to induce Anopheles to bite until at least six days after leaving the pupa." Nuttall and Shipley,[2] on the other hand, affirm that they have seen A. maculipennis feed after twenty-four hours. Individual differences doubtless exist.

Females that have been kept in the ice-box will, when brought into a room, usually bite eagerly as often as every four or five days. On several occasions we observed females to bite after eggs had been laid. In one case a female A. punctipennis would not bite between August 23 and September 1. Then biting occurred on September 1, just after the laying of one set of eggs.

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[1] *Loc. cit.*, p. 580.

[2] *Jour. of Hyg.*, 1, p. 465.

A second set was laid on September 3 and a third on September 6, but this female refused to bite again and died in a few hours. After the females are enfeebled by egg-laying it may happen that although attempting to bite they fail to draw blood.

EGG-LAYING, ETC.

Captured females of A. maculipennis usually laid, if at all, within twenty-four hours to two weeks after being taken. One, however, laid only after thirty-nine days of captivity. In most cases masses of over 100 eggs were deposited. The largest number observed in any one laying was 230, and the smallest 7. Other layings were 140, 127, 153, 16, 214, 71, 27, 142, 153, 62, 63. The numbers range higher than those recorded by most European observers of this species. It often happened that captured females died after a few days' confinement without laying, although the abdomen was distended with eggs. Sometimes one female laid several sets of eggs at intervals of two or three days. This was observed more frequently in A. punctipennis than in A. maculipennis. The number of eggs laid by A. punctipennis averaged considerably less than the number laid by A. maculipennis. This may be a specific difference.

Eggs were laid by nine females (A. maculipennis) at a low temperature in the ice-box (10°). In several instances the number deposited was small, but in the majority of cases masses of eggs were obtained as large as at ordinary temperatures. This is a point worth noting in view of the resistance of the eggs to low temperature.

Eggs laid in the ice-box were kept at a low temperature for ten days; when placed at room temperature they hatched in about two days. Eggs that have begun to develop proceed slowly, even at 10°. One set laid at room temperature and allowed to remain for twenty-four hours before transfer to the ice-box hatched in the ice-box after a few days.

The females usually die within twenty-four hours after laying, particularly if the oviposition is complete, i. e., 100–200 eggs. Occasionally one may survive for several days; the maximum longevity observed after oviposition was seven days.

COLOR PREFERENCES OF A. PUNCTIPENNIS.

Experiments were made to determine the color preference of adult A. punctipennis. The conditions of the experiment were substantially the same as those in a similar series of observations made by Nuttall[1] upon A. maculipennis. The mosquitoes were confined under a large hood with glass sides and front. Boxes covered with different colored cloths of similar texture were placed under the hood, and every day at a fixed hour during a week the number of mosquitoes that had settled on each color was counted. The position of the boxes was changed every day after counting to eliminate possible influences of light and shade and other factors. The results were as follows:

TABLE VIII.

Number of Mosquitoes	On
61	Dark red
57	Dark blue
41	Black
8	Dark pink
6	Dark green
5	Lavender
5	Purple
4	White
2	Light blue
2	Pale green
1	Light pink
0	Yellow

These results with A. punctipennis are very much like those obtained by Nuttall with A. maculipennis, dark red and dark blue proving the most attractive in both cases.

EFFECT OF LOW TEMPERATURE.

Anopheles maculipennis eggs, larvæ and imagoes were subjected to temperatures below freezing (—5° to —10° C.), the cold being produced by mixtures of ice and salt.

a) Eggs that were frozen into a solid block of ice for one hour and then placed at room temperature hatched as usual on the third day after the experiment, only three hours later than control eggs which had remained constantly at room temperature. In another experiment, the low temperature (—5° to —10° C.) was maintained for twenty-four hours. When these eggs were thawed out and placed at the ordinary room temperature, they hatched only twenty-four hours later than the control.

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[1] *Jour. of Hyg.*, 1902, 2, p. 74.

b) Larvæ of assorted sizes frozen in the same way did not revive on thawing.

c) Imagoes placed in a dry test-tube and subjected to the same temperature (for one hour and for twenty-four hours) were rendered numb and inactive, but on being restored to room temperature, revived, were ready to bite, and lived for several days —in one case for eight days.

The considerable resistance to cold displayed by the eggs indicates the possibility of occasional hibernation in this stage.